17 Leaf photosynthesis

17.1 Chapter summary

Photosynthesis is the process by which light energy is absorbed by green plants and used to produce carbohydrates from CO_2 and water. Photosynthesis is the means by which plants absorb carbon from the atmosphere, but in doing so water is lost as transpiration. Hence, the cycling of energy, water, and carbon between land and atmosphere are inextricably linked. Photosynthesis consists of three separate processes: light reactions, which convert light energy into chemical energy; dark reactions, which use this chemical energy to reduce CO_2 to carbohydrates; and diffusion, in which stomata open to allow CO_2 to diffuse into leaves from the surrounding air. The biological benefits gained by maximizing carbon uptake while minimizing water loss and the costly investment of resources in photosynthetic apparatus give rise to a wide variety of plant physiologies. This is seen in the differing C_3, C_4, and CAM photosynthetic pathways. It is also seen in the close matching of photosynthetic capacity and leaf traits to environment. Maximum photosynthetic capacity increases with decreasing leaf lifespan, increasing leaf nitrogen, and increasing specific leaf area. These relationships represent interdependent leaf traits that are a tradeoff between high metabolism and persistence.

17.2 Overview

Photosynthesis is the process in which light energy is absorbed by green plants and used to produce carbohydrates from CO_2 and water. The overall chemical reaction is

$$n\mathrm{CO_2} + 2n\mathrm{H_2O} \xrightarrow{\text{light}} (\mathrm{CH_2O})_n + n\mathrm{O_2} + n\mathrm{H_2O} \quad (17.1)$$

where n is the number of molecules of CO_2 that combine with water to form the carbohydrate $(CH_2O)_n$, releasing n molecules of oxygen to the atmosphere. The compound $(CH_2O)_n$ is not real but rather represents the general structure of a carbohydrate. Carbohydrates are sugars, starches and other related compounds containing carbon combined with hydrogen and oxygen. They are the most abundant organic compounds in nature and provide energy, structural material, and the building blocks for other molecules.

The biochemistry of photosynthesis is much more complicated than represented in this simple equation. It consists of three separate processes: light reactions, which convert light energy into chemical energy; dark reactions, which use this chemical energy to reduce CO_2 to carbohydrates; and diffusion, in which stomata open to allow CO_2 to diffuse into leaves from the surrounding air.

Photosynthesis occurs in the chloroplasts of leaves. These are disk-shaped structures within plant cells that are usually 5–10 μm in diameter. They consist of stroma, a gel-like material containing enzymes to convert CO_2 to carbohydrates during the dark reactions, and thylakoids, which are embedded throughout the stroma and are the site of the light reactions. The membranes of thylakoids contain the chlorophyll and carotenoid pigments essential to photosynthesis. A single leaf mesophyll cell may contain 50 chloroplasts and a square millimeter of leaf area may contain some 500 000 chloroplasts.

17.3 Light reactions

The light reactions convert light energy into the chemical energy required for the dark reactions. Absorption of light oxidizes water, providing electrons to create chemical energy and releasing oxygen. The electrons are passed through a series of biochemical reactions to $NADP^+$ (oxidized nicotinamide adenine dinucleotide phosphate) where they are temporarily stored in NADPH (reduced nicotinamide adenine dinucleotide phosphate) before being passed to CO_2 to form carbohydrates. In the process of electron transfer, chemical energy in the form of ATP (adenosine triphosphate) is created from adenosine diphosphate

(ADP) and inorganic phosphate (e.g., H_2PO_4, which is generically represented as P_i).

The first step in photosynthesis is the absorption of light by pigment molecules contained in chloroplasts. Light energy is transferred in discrete units called photons or quanta. The energy of a photon decreases as its wavelength increases (equation 3.2). The energy of a photon of red light with a wavelength of 0.680 μm is 2.92×10^{-19} J. One mole of photons (6.023×10^{23} photons) contains 176 000 J. For photosynthesis, the number of photons, not the total energy, is important. A photon of light with a blue wavelength (e.g., 0.450 μm) has more energy than a photon of light in the red range of the spectrum, but both have the same effect on photosynthesis. However, plants do not utilize the full spectrum of solar radiation for photosynthesis. Only radiation with wavelengths between 0.4 and 0.7 μm, known as photosynthetically active radiation, is used. Sunlight at higher wavelengths (i.e., the near-infrared waveband) is not utilized during photosynthesis. Instead, this radiation is reflected to prevent overheating.

Chlorophyll is the main pigment that makes leaves green, absorbing light primarily in the violet, blue, and red wavelengths while reflecting light in green wavelengths. Another class of pigments involved in photosynthesis is the carotenoids. These are red, orange, and yellow colored pigment molecules. The more abundant chlorophyll masks their color, which is why leaves are green. Chlorophyll and carotenoid pigments are embedded within chloroplasts in units of several hundred pigment molecules called photosystems. Light energy absorbed by a pigment molecule is transferred within the photosystem from one pigment molecule to the next until it reaches a reaction center. This is a special chlorophyll molecule that boosts one of its electrons to a higher energy level when light energy is absorbed. This electron is transferred to an acceptor molecule, initiating a series of biochemical reactions that create reducing power in the form of NADPH and chemical energy in the form of ATP. Plants have two separate groups of photosystems. Photosystem I (PS I) has optimal light absorption at a wavelength of 0.700 μm. Its reaction center is known as the P700 chlorophyll pigment molecule. Photosystem II (PS II) has optimal light absorption at 0.680 μm. Its reaction center is the P680 chlorophyll pigment molecule. Both are cooperatively involved in the light reactions of photosynthesis, using light energy to oxidize water and transfer its two electrons to NADPH.

The light reactions begin when light energy transferred to the P680 reaction center in PS II causes it to lose an electron (Fig. 17.1). This electron is transferred to an electron acceptor molecule. The electron-deficient P680 molecule replaces its electron by extracting an electron from water. This splits one water molecule (H_2O) into two protons ($2H^+$), two electrons ($2e^-$), and oxygen ($\frac{1}{2}$ O_2). The electron from P680 is passed through a series of biochemical reactions to the P700 chlorophyll reaction center in PS I. The P700 pigment molecule cannot accept an electron unless it has lost one. As with PS II, this occurs when light energy absorbed by surrounding pigment molecules is passed to the reaction center and an electron is boosted to an electron acceptor. This electron is then used to reduce $NADP^+$ to NADPH. Two electrons are required to reduce $NADP^+$ to NADPH. These are provided when one water molecule is split. The transfer of one electron from water to $NADP^+$ requires two photons (each photosystem must be excited). Since two electrons are required to reduce $NADP^+$ to NADPH, four photons are needed to pass two electrons from one water molecule to reduce one $NADP^+$ molecule. Two NADPH are needed in the dark reactions to reduce one CO_2 molecule. Consequently, eight photons are needed to split two water molecules, which provide the four electrons to produce the two NADPH needed to reduce one CO_2 molecule.

The biochemical reactions that transfer an electron from PS II to PS I also result in the formation of ATP in a process called photophosphorylation (Fig. 17.1). Some of this ATP is created during non-cyclic photophosphorylation when electrons are passed from PS II to PS I. In addition, light absorbed by PS I can initiate electron transport in which an electron is transferred to the electron acceptor and then passed back to P700. In this cyclic photophosphorylation, no water is split and no NADPH is formed but ATP is produced. An additional photon absorbed only by PS I is required for cyclic photophosphorylation, which together with non-cyclic photophosphorylation produces the three ATP molecules required in the dark reactions. The dark reactions can possibly require four ATP molecules, in which case three more photons must be absorbed by PS I only to form an additional ATP molecule. Hence, a total of nine to 12 photons must be absorbed to yield two NADPH and three or four ATP to reduce one molecule of CO_2 during the dark reactions.

17.4 Dark reactions

In the dark reactions, NADPH and ATP are used to fix CO_2 into a carbohydrate. Light is not directly involved. In many plants, the first product formed from CO_2 contains three carbon atoms. Hence, this is known as the C_3 photosynthetic pathway. The biochemical reactions that reduce CO_2 to carbohydrates are collectively known as the Calvin cycle and consist of three phases: carboxylation, reduction, and regeneration (Fig. 17.2). In the carboxylation phase, the

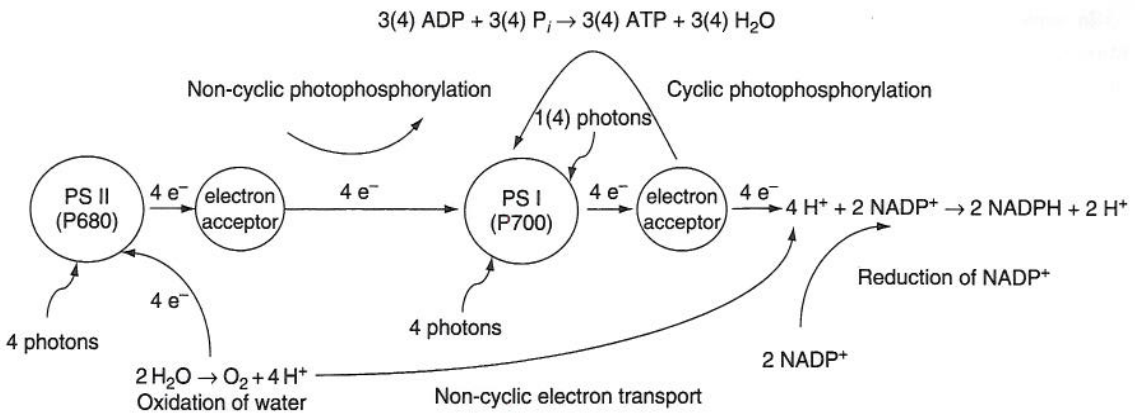

FIGURE 17.1. Light reactions of photosynthesis showing the various processes that produce the two NADPH and three ATP needed to reduce one CO_2 molecule: absorption of four photons each by PS II and PS I; transfer of four electrons from PS II to an acceptor molecule; oxidation of two water molecules by P680 to obtain four electrons; electron transport resulting in non-cyclic photophosphorylation and transfer of four hydrogen to $NADP^+$; electron transfer from PS I to an electron acceptor; reduction of $NADP^+$; and cyclic photophosphorylation. Numbers in parentheses show reactions when four ATP molecules are created instead of three.

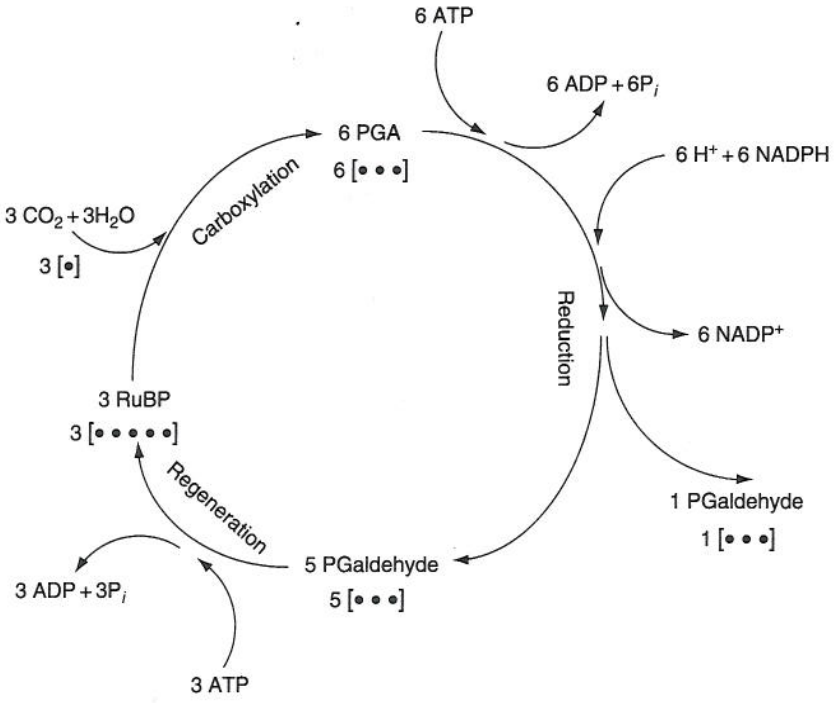

FIGURE 17.2. Dark reactions of the C_3 photosynthetic pathway. Three turns of the Calvin cycle are depicted. The symbol [•] indicates the number of carbon atoms contained in the compound.

5-carbon sugar ribulose-1,5-bisphosphate (RuBP) combines with CO_2 and water to form two 3-carbon compounds known as phosphoglyceric acid (PGA). This reaction is catalyzed by the enzyme ribulose bisphosphate carboxylase-oxygenase (rubisco). In the reduction phase, PGA is reduced to the 3-carbon compound phosphoglyceraldehyde (PGaldehyde) when inorganic phosphate is obtained from ATP and electrons are obtained from NADPH. The ADP and $NADP^+$ released in these reactions are converted back to ATP and NADPH during the light reactions. Some of the PGaldehyde is used to produce carbohydrates. The remainder is utilized in the regeneration phase, where it combines with additional ATP to regenerate RuBP. Three turns of the cycle fix three CO_2 molecules for a net production of one PGaldehyde. For each CO_2 fixed, two NADPH and three ATP are required.

In some plants such as corn, sugar cane, and most tropical grasses, CO_2 is first fixed into 4-carbon acids (malic and aspartic acids) rather than the 3-carbon PGA. These species are known as C_4 plants. In this pathway, CO_2 combines with phosphoenolpyruvate (PEP) in a reaction catalyzed by the enzyme PEP carboxylase. The resulting 4-carbon compound, oxaloacetate, is then converted to malate or aspartate. These acids are decarboxylated to yield CO_2 and pyruvate. The CO_2 enters the Calvin cycle, reacting with RuBP to form PGA, while the pyruvate reacts with ATP to form more PEP. The C_4 photosynthetic pathway requires a special leaf anatomy because the initial fixing of CO_2 into malate or aspartate occurs in different leaf cells (mesophyll cells) than the Calvin cycle (bundle-sheath cells). It also requires two more ATP in addition to the three already required in the Calvin cycle. These synthesize PEP for continued CO_2 fixation.

At first glance, the C_4 pathway seems inefficient and energetically expensive. In fact, however, C_4 plants are much more efficient at photosynthesis than C_3 plants. In the C_3 pathway, plants lose some of the CO_2 they fix in a light-enhanced process called photorespiration. This occurs because rubisco, which catalyzes CO_2 fixation by RuBP, also catalyzes the oxidation of RuBP by oxygen. This reaction consumes oxygen and releases CO_2 so that the net CO_2 uptake during photosynthesis is reduced by 30–50%. The rate of photorespiration depends on the ratio of CO_2:O_2 at the site of the dark reactions. In C_4 plants, the spatial separation of initial CO_2 fixation (mesophyll cells) and the Calvin cycle (bundle-sheath cells) creates a high CO_2:O_2 ratio at the site of CO_2 fixation into PGA during the Calvin cycle. With relatively little O_2 compared with CO_2 in bundle-sheath cells, RuBP is not oxidized by oxygen. The C_4 plants, therefore, have little or no photorespiration and consequently have greater net photosynthetic rates than C_3 plants at high light levels and warm temperatures.

Many succulent plants such as cacti, orchids, and bromeliads use a third photosynthetic pathway called crassulacean acid metabolism (CAM). These plants grow in hot, arid regions. In this environment, they cannot open their stomata during the day to obtain CO_2 because they would quickly be desiccated by transpiration. Instead, stomata open at night, when temperatures are cooler, and CO_2 is fixed by PEP to form malic acid. The malic acid accumulates during the night. During daylight, it is decarboxylated to release CO_2 that is then refixed in the Calvin cycle. Unlike C_4 plants, with their spatial separation of CO_2 fixation by PEP and carbohydrate synthesis during the Calvin cycle, CO_2 fixation and the Calvin cycle take place in the same cell. Instead, night and day temporally separate the two processes.

17.5 Stomata

For photosynthesis to occur, CO_2 in the air surrounding a leaf must diffuse into the leaf to the chloroplasts, where it is fixed and converted to carbohydrates. Most leaves have a waxy layer on the surface that restricts gas diffusion. Instead, CO_2 passes through microscopic openings in foliage known as stomata. Stomata are typically 10–80 μm in length with a maximum width of about 5 μm (Larcher 1995, p. 81; Hetherington and Woodward 2003). A leaf may contain 5–1000 stomata per square millimeter of leaf area with a total pore area of less than 1–5% of leaf area. Stomatal conductance for CO_2 and water is directly proportional to pore width, with the maximum opening determining the upper limit to the rate of gas exchange. By varying the width of the stomatal pore, plants control gas exchange. Stomata open to allow CO_2 uptake during photosynthesis and close to prevent desiccation during transpiration.

The rate of leaf photosynthesis can be represented as a diffusion process:

$$A = \frac{c_a - c_s}{(1.37r_b)P} = \frac{c_s - c_i}{(1.65r_s)P} = \frac{c_a - c_i}{(1.37r_b + 1.65r_s)P} \tag{17.2}$$

In these equations, c_a, c_s, and c_i are the ambient, leaf surface, and internal CO_2 partial pressures (Pa), respectively, P is atmospheric pressure (Pa), and r_b and r_s are leaf boundary layer and stomatal resistances to water vapor diffusion ($s\,m^2\,\mu mol^{-1}$ H_2O), respectively. The factors 1.37 and 1.65 are the ratios of the diffusivity of CO_2 to water for leaf boundary layer and stomatal resistances, respectively, and account for the different diffusivity of CO_2 and water. The first equation represents the diffusion of CO_2 from air surrounding a leaf to the leaf surface, which is inversely proportional to leaf boundary layer resistance. The second equation is the diffusion of CO_2 from the leaf surface to inside the leaf, which is inversely proportional to stomatal resistance. The final equation is the combined CO_2 flux from air to inside a leaf.

Stomata open and close in response to a variety of environmental factors (Fig. 17.3). Light has a strong influence. Except for CAM plants, stomata open with light and close in darkness. Stomata also close with temperatures warmer and colder than some optimal value. Stomata close to prevent excessive water loss. This occurs in two ways. First, stomatal conductance decreases as leaf water potential decreases. Low leaf water potential occurs when the loss of water by transpiration exceeds the rate of uptake from soil. Stomata close to prevent further desiccation. Second, the vapor pressure deficit between the leaf and air increases as the humidity of air decreases, creating a

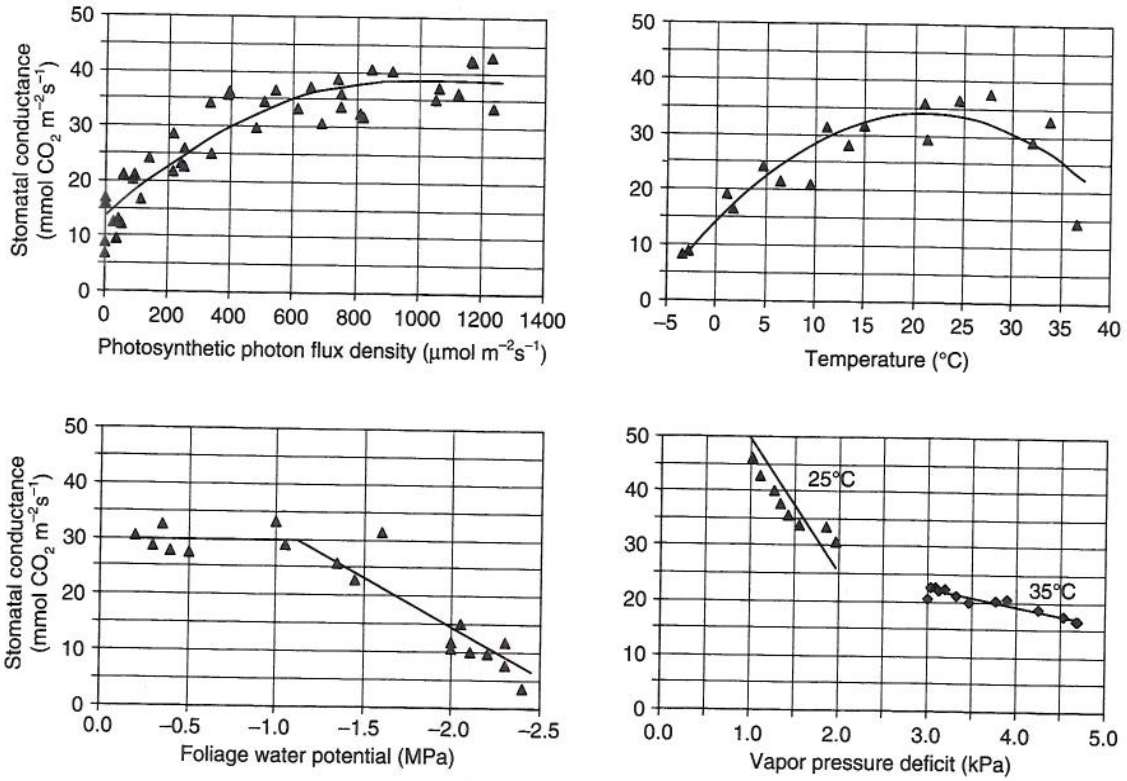

FIGURE 17.3. Environmental controls of stomatal conductance for jack pine (*Pinus banksiana*) trees. Stomatal conductance is shown in response to photosynthetic photon flux density (top left), temperature (top right), foliage water potential (bottom left), and vapor pressure deficit (bottom right). Data from Dang *et al.* (1997a, b, 1998).

high potential for transpiration. Stomata close to prevent excessive desiccation under these conditions.

Jarvis (1976) developed an empirical model of stomatal conductance:

$$g_s = g_s(\phi) f_1(T) f_2(VPD) f_3(\psi) f_4(C_a) \qquad (17.3)$$

where $g_s(\phi)$ is stomatal conductance as a function of photosynthetically active radiation, and $f_1(T)$, $f_2(VPD)$, $f_3(\psi)$, and $f_4(C_a)$ are empirical functions scaled from zero to one that adjust stomatal conductance for temperature, vapor pressure deficit, foliage water potential, and ambient CO_2 concentration, respectively. This approach has been used to represent stomatal conductance in the land surface models used with climate models (Dickinson *et al.* 1986, 1993; Sellers *et al.* 1986).

17.6 Net photosynthesis

At the same time as leaves absorb CO_2 during photosynthesis, they release CO_2 in respiration. Respiration is the complement of photosynthesis. It is the process by which organic compounds are oxidized to produce the energy needed to maintain plant functions and grow new plant tissues. For glucose, the overall chemical reaction is

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O \qquad (17.4)$$

The rate of respiration depends on the biochemical quality of the tissue and increases exponentially with warmer temperatures. This respiration is different from photorespiration, which is driven by fixation of oxygen rather than CO_2 by rubisco, and occurs simultaneously with photosynthesis in leaf cells. The difference between CO_2 uptake during photosynthesis and CO_2 loss during leaf respiration is the net CO_2 uptake by a leaf.

Figure 17.4 illustrates the effect of leaf respiration on net photosynthesis. At cold temperatures, photosynthesis and respiration are minimal, producing negligible net CO_2 uptake. As temperature increases above freezing, photosynthetic uptake and respiration loss increase as a result of temperature activation of enzymes. However, uptake exceeds loss for a net CO_2 gain. As temperature increases further, photosynthesis attains a maximum rate and then declines. Greater respiration at high temperatures contributes to the decline in net photosynthesis. In addition, both

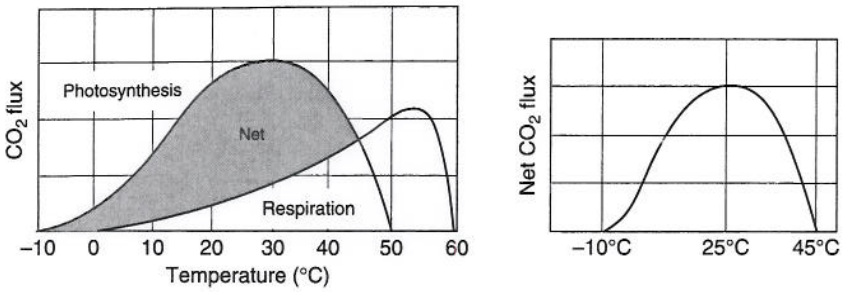

FIGURE 17.4. Effect of temperature on photosynthesis and respiration in C_3 plants.

photosynthesis and respiration are inhibited by high temperature. As a result, net photosynthesis shows a parabolic response to temperature defined by three cardinal values: the minimum and maximum temperatures at which there is no net CO_2 gain and a temperature at which CO_2 uptake is optimal.

A variety of environmental factors influence net photosynthesis (Fig. 17.5). Because of its role in the light reactions, light is an essential factor that limits the rate of photosynthesis. If a leaf absorbs insufficient light, there will not be enough ATP and NADPH to fuel the dark reactions. When the irradiance is below a certain level, typically about 10–40 μmol photons $m^{-2} s^{-1}$, CO_2 uptake during photosynthesis is balanced by CO_2 loss during respiration; net assimilation is zero. Only when light levels are above this light compensation point does a leaf gain carbon. Photosynthetic rates increase with greater irradiance until light saturation, when increased light no longer increases photosynthesis. At these high light levels, the rate of photosynthesis is not limited by light but rather by the amount of CO_2 and rubisco available for the dark reactions.

Temperature affects photosynthesis because sufficient, but not excessive, heat is a prerequisite for biochemical reactions (Fig. 17.5). Photosynthesis is restricted to a certain temperature range beyond which biological activity is inhibited. Within this range, photosynthesis increases up to an optimal temperature, beyond which it begins to decrease. The optimum temperature range for most C_3 plants is 15–30 °C, but the temperature range over which plants can photosynthesize is quite large. Many plants can photosynthesize with temperatures below freezing or in excess of 40 °C (Larcher 1995, p. 109). Desert plants have higher temperature optima than arctic or alpine plants.

The rate of photosynthesis decreases as a leaf becomes desiccated and its foliage water potential decreases (Fig. 17.5). When transpiration exceeds root uptake, plants can become desiccated. Cells lose turgor. Leaves wither and become limp. Absorption of soil nutrients and translocation of photosynthetic products within the plant are inhibited. Because water is so essential, photosynthesis decreases sharply when the leaf water content falls below some minimal value and stomata close. Stomata also close with high vapor pressure deficit to reduce water loss during transpiration (Fig. 17.5).

Photosynthetic rates are enhanced by higher concentration of CO_2 in the air (Fig. 17.5). In C_3 plants, the additional CO_2 reduces photorespiration by increasing the ratio of CO_2:O_2 reacting with rubisco. Similar to light, the rate of photosynthesis increases with higher CO_2 concentrations up to a saturation point, beyond which photosynthesis remains constant. At this point, photosynthesis is not limited by the amount of CO_2 available for fixation but rather by the supply of NADPH and ATP from the light reactions. The rate of photosynthesis decreases markedly with low CO_2 concentrations, when the supply of CO_2 limits photosynthesis. At the CO_2 compensation point, which typically ranges from 30 to 50 ppm, the rate of CO_2 uptake during photosynthesis is balanced by CO_2 loss during respiration so that there is no net gain of CO_2 by the leaf. In C_3 plants, there is a strong photosynthetic interaction between light and CO_2. High irradiance increases net photosynthesis more at high CO_2 concentrations than at low concentrations, and CO_2 saturation requires higher CO_2 concentrations at high irradiance than at low light. Conversely, C_4 plants saturate with CO_2 concentrations of about 400 ppm regardless of light. They also have a lower compensation point (about 10 ppm) than C_3 plants.

The rate of photosynthesis increases with increasing amounts of nitrogen in foliage (Fig. 17.5). Nitrogen is an essential component of chlorophyll and rubisco. Greater amounts of nitrogen allow for more chlorophyll and rubisco, fueling greater rates of photosynthesis.

These photosynthetic responses to environmental conditions vary greatly among plants. Table 17.1 compares maximum photosynthetic rates under optimal conditions for several plant types. Among herbaceous plants, those utilizing the C_4 pathway generally have the highest maximum photosynthetic rates; CAM plants generally have the lowest rates. Trees, which utilize the C_3 pathway, generally have low rates of maximum photosynthesis. Table 17.2

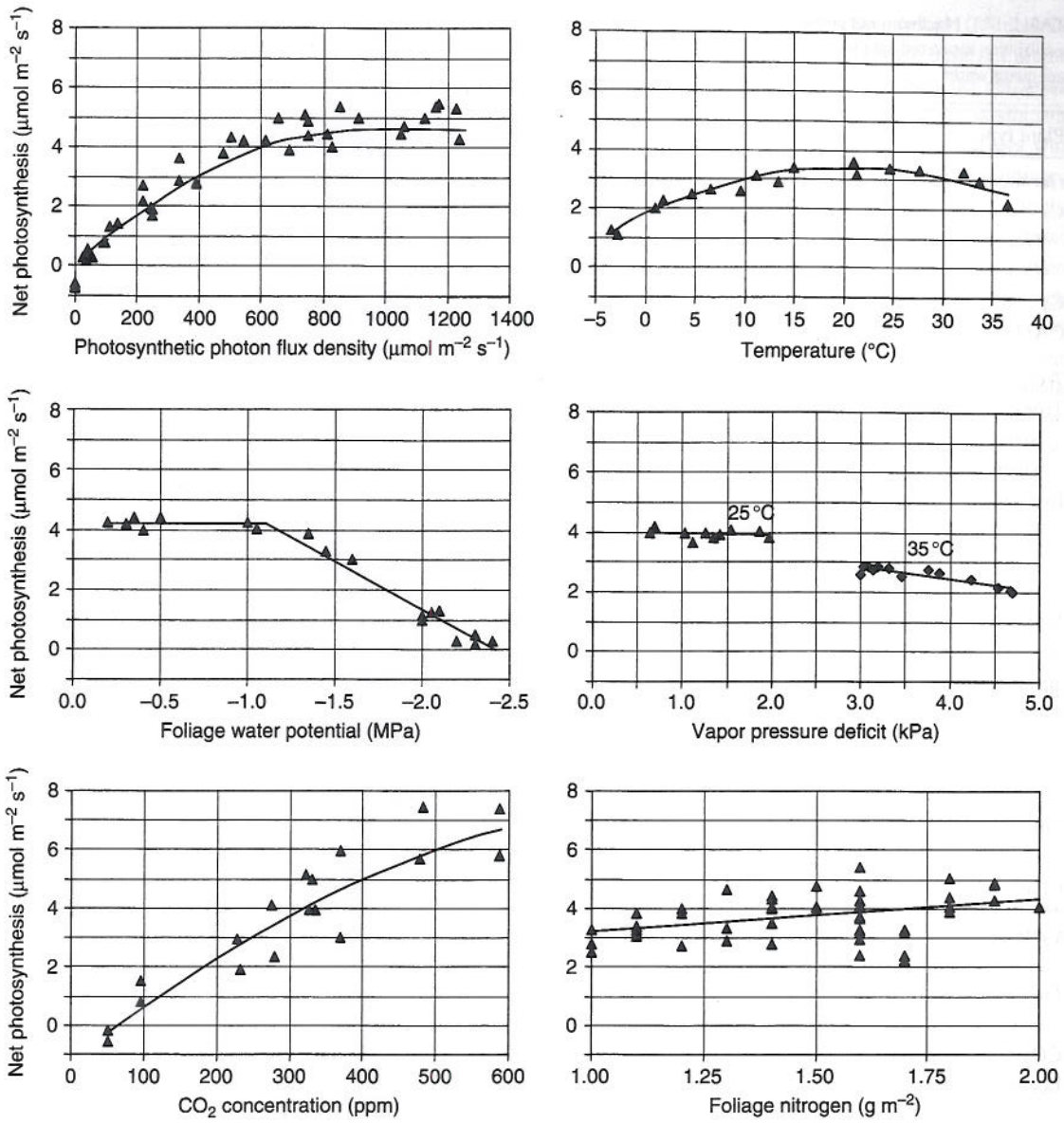

FIG. 17.5. Environmental controls of net photosynthesis for jack pine trees. Net photosynthesis is shown in response to photosynthetic photon flux density (top left), temperature (top right), foliage water potential (middle left), vapor pressure deficit (middle right), ambient CO_2 concentration (bottom left), and foliage nitrogen (bottom right). Data from Dang *et al.* (1997a, b, 1998).

compares the characteristics of the C_3, C_4, and CAM photosynthetic pathways. One of the major differences is the presence of photorespiration in C_3 plants and absence in C_4 plants. Competition between oxygen and CO_2 for rubisco means that increasing concentration of oxygen in the atmosphere inhibits CO_2 uptake during C_3 photosynthesis and that this inhibition is greater at lower CO_2 concentration. Hence, photosynthesis in C_3 plants is often limited by ambient CO_2 concentrations while that of C_4 plants is much less limited by CO_2. The lower CO_2 compensation point in C_4 and CAM plants compared with C_3 plants is a result of CO_2 fixation by PEP carboxylase, which has a high affinity for CO_2, and because of low photorespiration. Plants utilizing the C_4 photosynthetic pathway show little light saturation and at full sunlight can have photosynthetic rates twice that of a C_3 plant. Because of their more efficient use of CO_2, C_4 plants attain similar or greater photosynthetic rates as C_3 plants with less water loss.

TABLE 17.1. Maximum net photosynthesis with natural CO_2 availability, saturated light intensity, optimal temperature, and adequate water

Plant type	CO_2 uptake ($\mu mol\ m^{-2}\ s^{-1}$)
Herbaceous	
C_3	
Grasses	5–15
Crops	20–40
C_4	30–60
CAM	5–10
Tree	
Tropical broadleaf evergreen	
Sunlit leaves	10–16
Shaded leaves	5–7
Broadleaf deciduous	
Sunlit leaves	10–15
Shaded leaves	3–6
Needleleaf evergreen	3–6
Needleleaf deciduous	8–10

Source. Data from Larcher (1995, pp. 85–86). See also Schulze *et al.* (1994) and Woodward and Smith (1994).

Hence, they have higher water use efficiency, defined as the dry matter produced for a given amount of water lost in transpiration. In addition, the optimal temperature for C_4 plants is higher than that of C_3 plants. These features allow C_4 plants to grow well in warm regions with periodic drought such as tropical savanna.

17.7 Photosynthesis–transpiration compromise

The physiology of stomata has evolved as a compromise between the two conflicting goals of permitting CO_2 uptake during photosynthesis while restricting water loss during transpiration (Cowan 1977). Stomata are regulated so as to maximize carbon gain and minimize water loss. This is evident from experiments relating stomatal conductance, photosynthesis, and transpiration. Plants grown under a variety of irradiances, nutrient concentrations, ambient CO_2 concentrations, and leaf water potentials show large variation in photosynthetic rate and stomatal conductance, but photosynthesis and stomatal conductance vary in near constant proportion (Wong *et al.* 1979, 1985a–c). Photosynthesis and stomatal conductance measurements

TABLE 17.2. Photosynthetic characteristics of C_3, C_4, and CAM plants

Characteristic	C_3 plants	C_4 plants	CAM plants
Carboxylating enzyme	Rubisco	PEP carboxylase and rubisco	Dark: PEP carboxylase Light: rubisco
First product of photosynthesis	3-carbon acid (PGA)	4-carbon acids (oxaloacetate, malate, aspartate)	Dark: malate Light: PGA
CO_2:ATP:NADPH	1:3:2	1:5:2	1:6.5:2
Location of processes	Mesophyll cells	Mesophyll cells then bundle-sheath cells	Mesophyll cells
Stomatal behavior	Open during day, close at night	Open during day, close at night	Close during day, open at night
Photorespiration	High	Low	Low
Photosynthesis inhibited by 21% O_2	Yes	No	Yes
Photosynthetic capacity	Low to high	High to very high	Medium
Light saturation	Intermediate intensity	No saturation	Intermediate to high intensity
Water use efficiency	1–5 $g\ kg^{-1}\ H_2O$	3–5 $g\ kg^{-1}\ H_2O$	6–15 $g\ kg^{-1}\ H_2O$
Optimum temperature for photosynthesis	15–25 °C	30–45 °C	30–35 °C
CO_2 compensation point	30–50 ppm	0–10 ppm	0–5 ppm

Source. Data from Larcher (1995, p. 64, p. 98, p. 109, p. 122), Salisbury and Ross (1992, p. 257), and Barbour *et al.* (1999, pp. 421–422).

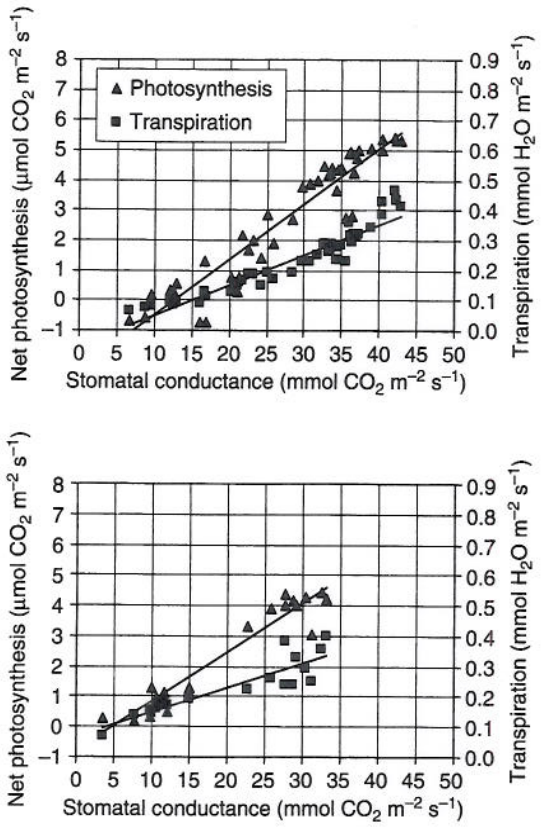

FIGURE 17.6. Relationship between photosynthesis, transpiration, and stomatal conductance for jack pine trees. Top: light response over a range of 0–1250 μmol photons $m^{-2} s^{-1}$. Bottom: foliage water potential response over a range of –0.2 to –2.4 MPa. Data from Dang *et al.* (1997a, b, 1998).

for jack pine trees illustrate such relationships. Over a wide range of light and foliage water potential, from full illumination to dark and from moist to desiccated, net photosynthesis increases proportionally with increases in stomatal conductance (Fig. 17.6). Transpiration also increases with greater conductance. Physiological measurements among a variety of plant communities also show a positive correlation between maximum stomatal conductance and maximum rate of photosynthesis, though the relationship differs among plant functional types (Schulze and Hall 1982; Field and Mooney 1986; Körner 1994; Schulze *et al.* 1994; Hetherington and Woodward 2003) (Fig. 17.7). Coherent changes in photosynthetic carbon metabolism and stomatal behavior suggest they change in concert. Stomatal conductance varies to match the photosynthetic capacity of leaves as determined by site conditions and plant physiology so as to minimize the rate of transpiration.

17.8 A photosynthesis–stomatal conductance model

Leaf photosynthesis can be represented by a biochemical model based on the enzyme kinetics of rubisco and the regeneration of RuBP in response to the supply of NADPH and ATP produced in the light reactions (Farquhar *et al.* 1980; Farquhar and von Caemmerer 1982; Farquhar 1989). In this model, photosynthesis is the lesser of two rates:

$$A_n = \min(w_c, w_j) - R_d \qquad (17.5)$$

where w_c is the rubisco-limited rate of photosynthesis, w_j is light-limited rate allowed by RuBP regeneration, and R_d is

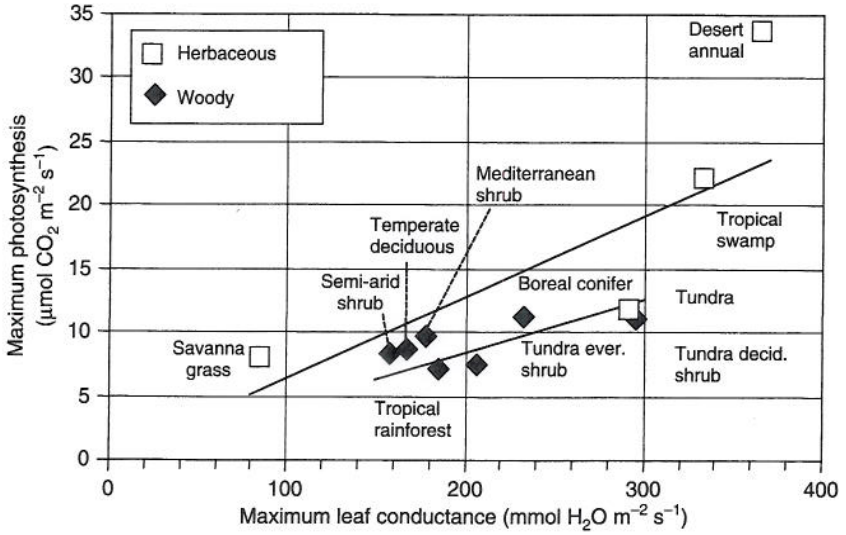

FIGURE 17.7. Relationship between maximum leaf conductance and maximum photosynthesis. Data shown are mean values for seven types of woody vegetation and four types of herbaceous vegetation. The regression equations shown with these data are based on the full dataset of 55 woody plants and 18 herbaceous plants. Data from Körner (1994).

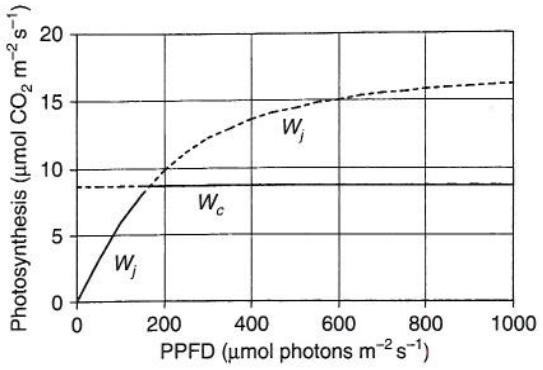

FIGURE 17.8. Photosynthetic light response curve showing the W_c and W_j rates of photosynthesis in relation to photosynthetic photon flux density (PPFD). The W_c-limited rate is 8.7 μmol CO_2 m^{-2} s^{-1}. The W_j-limited rate increases with light. Actual photosynthesis is the smaller of these two values. The transition from the W_j-limited to W_c-limited rate occurs at about 165 μmol photons m^{-2} s^{-1}. From a model by Bonan (1995).

dark respiration (all with units of μmol CO_2 m^{-2} s^{-1}). The rubisco-limited rate is

$$w_c = \frac{V_{\max}(c_i - \Gamma_*)}{c_i + K_c(1 + O_i/K_o)} \tag{17.6}$$

and the RuBP regeneration-limited rate is

$$w_j = \frac{J(c_i - \Gamma_*)}{4(c_i + 2\Gamma_*)} \tag{17.7}$$

where c_i is the partial pressure (Pa) of CO_2 in leaf chloroplast (also known as intercellular CO_2), Γ_* is the CO_2 compensation point (Pa), O_i is the partial pressure (Pa) of oxygen in leaf chloroplast (which is the same as that of ambient air, i.e., $0.209P$), and K_c and K_o are Michaelis–Menten constants (Pa) for the carboxylation and oxygenation of rubisco. The parameters Γ_*, K_c, and K_o depend on temperature. Typical values at 25 °C are $\Gamma_* = 2$–4 Pa, $K_c = 30$ Pa, and $K_o = 30\,000$ Pa. The potential rate of electron transport (J, μmol electrons m^{-2} s^{-1}) depends on the amount of photosynthetically active radiation absorbed by a leaf (ϕ, μmol photons m^{-2} s^{-1}) as the smaller of the two roots of the equation:

$$0.7J^2 - (J_{\max} + 0.385\phi)J + 0.385J_{\max}\phi = 0 \tag{17.8}$$

where $J_{\max}$ is the maximum potential rate of electron transport (μmol electrons m^{-2} s^{-1}). The maximum rate of carboxylation ($V_{\max}$, μmol CO_2 m^{-2} s^{-1}) is proportional to the amount of rubisco in the leaf. The maximum potential rate of electron transport ($J_{\max}$) varies in relation to leaf chlorophyll. The parameters $V_{\max}$ and $J_{\max}$ also depend on temperature. Figure 17.8 illustrates these two components of photosynthesis using typical parameter values. At light levels less than about 165 μmol photons m^{-2} s^{-1}, photosynthesis is limited by RuBP regeneration (W_j). Higher light levels increase photosynthesis as a result of greater ATP and NADPH production. The initial rate of increase of 0.067 μmol CO_2 per μmol photon is known as the quantum efficiency. As light increases, photosynthesis becomes limited by rubisco (W_c).

The physiology of stomata and the biophysics of transpiration are linked to the biochemistry of photosynthesis. Collatz *et al.* (1991) described one approach that links these processes. For C_3 plants, stomatal conductance (g_s, μmol H_2O m^{-2} s^{-1}) is related to net photosynthesis (A_n, μmol CO_2 m^{-2} s^{-1}):

$$\frac{1}{r_s} = g_s = m\frac{A_n(h_s/100)P}{c_s} + b \tag{17.9}$$

where m is a constant, h_s and c_s are the relative humidity (%) and CO_2 partial pressure (Pa) at the leaf surface, respectively, P is atmospheric pressure (Pa), and $b = 2000$ μmol m^{-2} s^{-1} is a typical minimum leaf conductance. A typical value is $m = 6$ for needleleaf trees and $m = 9$ for other plants. Collatz *et al.* (1992) described a similar model for C_4 plants.

Equation (17.9), with A_n from (17.5)–(17.7), can be used to model stomatal conductance. Solution of this set of equations describing leaf photosynthesis and stomatal conductance requires knowledge of intercellular CO_2 (c_i) and CO_2 at the leaf surface (c_s). These are obtained by representing photosynthesis as a diffusion process from the ambient air to the leaf surface, regulated by leaf boundary layer conductance, and from the leaf surface to intercellular space, regulated by stomatal conductance, as in (17.2). A similar resistance network is used to calculate relative humidity at the leaf surface (h_s). Solution of this equation set is complex and can involve iterative solutions to A_n and g_s or analytical solutions of a cubic equation for A_n (e.g., Baldocchi 1994; Su *et al.* 1996). This approach has been used to model photosynthesis and stomatal conductance in the land surface models used with climate models (Bonan 1995; Denning *et al.* 1995, 1996a, b; Sellers *et al.* 1996; Craig *et al.* 1998).

General insights to leaf physiology are readily apparent from these equations. For example, under low irradiance stomatal conductance should not be affected by changes in $V_{\max}$ because photosynthesis is limited by the rate of electron transport in the light reactions. At high irradiance, when photosynthesis is limited by rubisco, changes in $V_{\max}$ can alter stomatal conductance. Leaves growing in shaded environments achieve no photosynthetic gain by investing in the energetically expensive rubisco and thus have low $V_{\max}$. Sunlit leaves have high $V_{\max}$ so as to maximize the rate of photosynthesis.

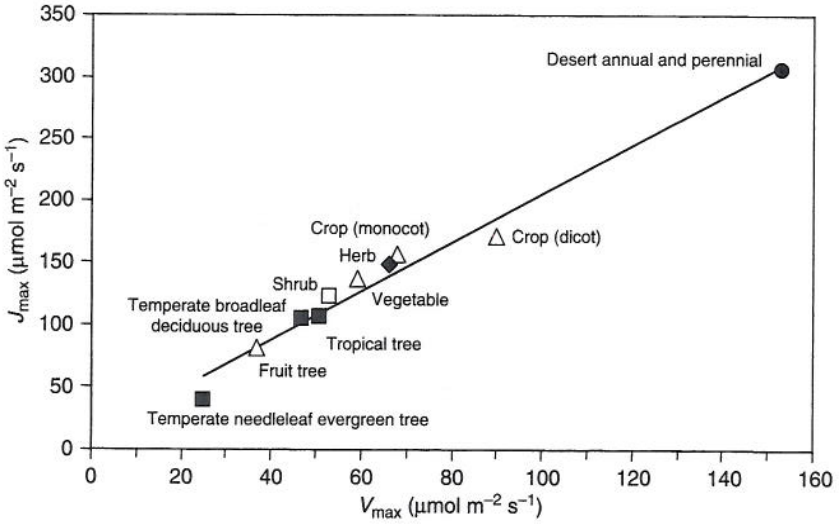

FIGURE 17.9. Relationship between maximum rate of carboxylation (V_{max}) and maximum potential rate of electron transport (J_{max}) for 109 C_3 species. Data are shown as averages for broad groups of species. Original data for all 109 species show a similar relationship. Data from Wullschleger (1993).

In addition, there is no need to have extra chlorophyll to trap light if the concentration of rubisco is low. Thus, leaves with low V_{max} should also have low J_{max}. Such a relationship has indeed been found in a study of 109 species of C_3 plants (Fig. 17.9). These species differ greatly in their biochemical capacity to assimilate CO_2. Estimates of V_{max} range from a low of 6 μmol CO_2 m^{-2} s^{-1} in some trees to a high of 194 μmol CO_2 m^{-2} s^{-1} for some agricultural crops. Desert annuals and perennials have the highest V_{max}. Monocotyledon crops such as wheat and rice and dicotyledon crops such as cotton, soybean, and tobacco also have high V_{max}. Temperate needleleaf evergreen trees have the lowest V_{max}. Values for J_{max} have a similar wide range, but there is a positive correlation between V_{max} and J_{max}. This reflects an optimal allocation of resources, especially nitrogen, to balance enzymatic (rubisco) and light-harvesting (chlorophyll) capabilities.

17.9 Coordinated leaf traits

The preceding discussions of stomatal conductance and photosynthesis suggest leaves have certain characteristics related to photosynthetic capacity. Indeed, studies of plants growing in a wide variety of plant communities and environments and representing a diversity of life forms repeatedly show coordinated relationships among leaf traits such as maximum photosynthetic capacity, maintenance respiration, nitrogen concentration, leaf lifespan, and the ratio of leaf surface area to leaf dry mass (specific leaf area). Photosynthetic capacity, respiration rate, and leaf nitrogen are interrelated because nitrogen is integral to the enzymes and pigments necessary for photosynthesis. Consequently, there is a strong relationship between maximum photosynthetic capacity and leaf nitrogen content (Field and Mooney 1986; Schulze *et al.* 1994; Peterson *et al.* 1999). Figure 17.10 illustrates this relationship for 22 broadleaf deciduous and 9 needleleaf evergreen temperate tree species. Needleleaf evergreen trees have a lower rate of photosynthesis for a similar range of leaf nitrogen than broadleaf deciduous trees. Moreover, the rate at which photosynthetic capacity increases in response to increased leaf nitrogen is less for needleleaf evergreen trees than for broadleaf deciduous trees.

Subsequent studies have emphasized correlations of leaf traits with specific leaf area and leaf longevity (Reich *et al.* 1992, 1995, 1997, 1998a, b; Westoby *et al.* 2002; Wright *et al.* 2004). Specific leaf area represents the leaf area produced per unit leaf dry mass. It is a measure of carbon (dry mass) investment in photosynthesizing leaf area. Species with high specific leaf area have thin leaves with a large surface area per unit mass (e.g., a broadleaf). Species with low specific leaf area have thick foliage with low surface area per unit mass (e.g., a needleleaf). Leaf longevity describes the period over which the initial investment in dry mass and nutrients to produce the leaf can be recouped during photosynthesis. Deciduous leaves are shed annually, and the cost to produce the leaf must be incurred every year. That investment cost can be recouped over longer periods in evergreen leaves.

Across a diversity of plant communities and environments, species with short leaf lifespan generally have high maximum photosynthetic capacity, high leaf nitrogen, and thin leaves with high surface area to mass. For example,

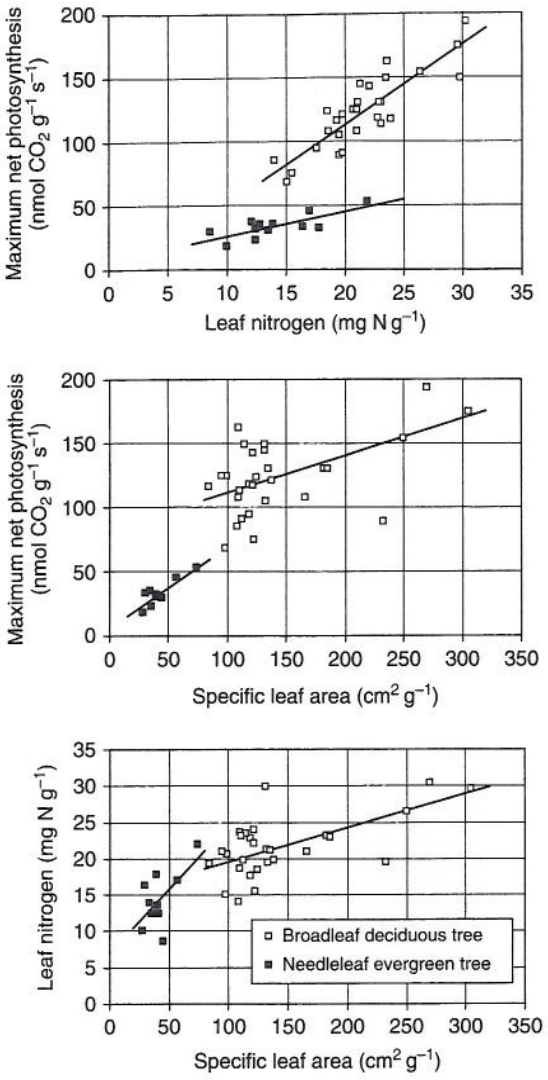

FIGURE 17.10. Coordinated leaf traits for 22 broadleaf deciduous and 9 needleleaf evergreen temperate tree species. Top: maximum rate of photosynthesis in relation to leaf nitrogen. Middle: maximum rate of photosynthesis in relation to leaf surface area per unit mass (specific leaf area). Bottom: leaf nitrogen in relation to specific leaf area. Data from Reich *et al.* (1995).

the long-lived needles of coniferous trees have a low surface area per unit mass (i.e., are thick) while broadleaf deciduous leaves are thin and have a high surface area per unit mass. Needleleaf evergreen trees have lower maximum photosynthetic capacity and specific leaf area than broadleaf deciduous trees for common nitrogen content (Fig. 17.10). Comparisons among additional plant functional groups show similar distinctions based on type of leaf (broadleaf, needleleaf) and leaf lifespan (deciduous, evergreen). In a study of 257 species, mean leaf traits differ among functional groups (Table 17.3). Forbs have the highest maximum photosynthetic capacity, leaf nitrogen, and specific leaf area. Woody species have lower values of these traits. Within woody species, additional distinction is based on leaf type (needleleaf, broadleaf) and longevity (deciduous or less than one-year lifespan, evergreen or greater than one-year lifespan). Evergreen species of shrubs, broadleaf trees, and needleleaf trees have lower maximum photosynthetic capacity, leaf nitrogen, and specific leaf area than corresponding deciduous species. The slope of the photosynthesis–nitrogen relationship (i.e., the photosynthetic capacity per unit mass of nitrogen) differs among functional groups. Forbs have the steepest slope; needleleaf evergreen trees have the shallowest slope. Among broadleaf shrubs and trees, short-lived deciduous leaves have a greater slope than long-lived evergreen leaves. Species with long lifespan and low specific leaf area, whether broadleaf or needleleaf, tend to have lower maximum photosynthetic rates per unit leaf nitrogen.

Leaf maintenance respiration is also related to photosynthetic capacity and leaf traits because a high photosynthetic capacity requires a large investment in enzymes and pigments, which have high maintenance respiration costs (Ryan 1991, 1995; Reich *et al.* 1998b). In a study of 69 species from four functional groups (forbs, broadleaf shrubs, broadleaf trees, needleleaf trees) ranging from alpine tundra to desert to tropical rainforest, leaf respiration rates at 25 °C increase with greater leaf nitrogen and specific leaf area and decrease with increased leaf longevity (Fig. 17.11). Respiration and leaf traits differ among functional groups (Table 17.4). Forbs have the highest respiration rate. Needleleaf evergreen trees have the lowest respiration rate. Broadleaf shrubs and trees are intermediate in their traits. Different relationships among functional groups are associated with differences in specific leaf area and leaf lifespan. Functional groups with a high specific leaf area and short leaf lifespan have high respiration rates at any given leaf nitrogen.

Wright *et al.* (2004) generalized these relationships in an analysis of 2548 species from 219 families at 175 locations worldwide including arctic tundra, boreal forest, tropical rainforest, grassland, and hot and cold deserts. Annual mean temperature ranged from −16.5 to 27.5 °C. Annual precipitation ranged from 133 to 5300 mm. Over this wide variety of plant communities, environments, and life forms, maximum photosynthetic capacity and leaf respiration rate increase with decreasing leaf lifespan, increasing leaf nitrogen, and increasing specific leaf area. They called this the "leaf economics spectrum," which ranges from quick to slow return on investments of carbon

TABLE 17.3. Maximum photosynthetic capacity, specific leaf area, leaf nitrogen, and slope for photosynthesis–nitrogen relationship for 257 species of forbs, shrubs, broadleaf trees, and needleleaf trees

Functional group	Photosynthetic capacity (nmol CO_2 g^{-1} s^{-1})	Specific leaf area (cm^2 g^{-1})	Leaf nitrogen (mg N g^{-1})	A_{max}-N slope (μmol CO_2 s^{-1} g^{-1} N)
Forb	305	197	35.4	9.24
Broadleaf shrub				
Deciduous	157	140	20.8	9.68
Evergreen	62	71	15.8	2.36
Broadleaf tree				
Deciduous	139	137	22.2	4.20
Evergreen	55	89	15.0	1.47
Needleleaf tree				
Deciduous	97	100	19.0	–
Evergreen	28	38	11.6	2.76

Source. Data from Reich *et al.* (1998a).

TABLE 17.4. Leaf maintenance respiration at 25 °C, specific leaf area, leaf nitrogen, and leaf lifespan for 69 species of forbs, broadleaf shrubs, broadleaf trees, and needleleaf trees

Functional group	Respiration (nmol CO_2 g^{-1} s^{-1})	Specific leaf area (cm^2 g^{-1})	Leaf nitrogen (mg N g^{-1})	Leaf longevity (months)
Forb	27.3	188	28.2	4.5
Broadleaf shrub	14.4	112	20.9	9.4
Broadleaf tree	11.4	112	19.2	13.3
Needleleaf tree	4.9	48	11.6	43.9

Source. Data from Reich *et al.* (1998b).

(dry mass) and nitrogen in leaves. Species with short-lived leaves generally have high specific leaf area (i.e., low carbon investment per unit leaf area), high leaf nitrogen, high photosynthetic capacity, and high maintenance respiration rate. They reap a quick return on investment. At the other end of the spectrum are species with long leaf lifespan, low specific leaf area, low leaf nitrogen, and low rates of photosynthesis and respiration. These leaves are expensive to produce and return that investment over a long period. In between is a continuum of leaves with coordinated traits scaled between these two extremes. These functional patterns of variation among leaf structure, longevity, nutrition, and metabolism represent interdependent leaf traits that are a tradeoff between high metabolism and persistence. Climate plays a much smaller role in determining variation among leaf traits (Wright *et al.* 2004, 2005).

17.10 Review questions

1. Why is light needed for photosynthesis?
2. What is photorespiration? Why are photorespiration rates lower in plants utilizing the C_4 photosynthetic pathway than in C_3 plants?
3. Why does photosynthesis saturate at high light levels in C_3 plants? How does this compare with the light response curve of C_4 plants?
4. Why does photosynthesis saturate at high ambient CO_2 concentrations in C_3 plants? How does this compare with the CO_2 response curve of C_4 plants?
5. Some grasses utilize the C_3 photosynthetic pathway; others are C_4 plants. What type of grass is favored in a CO_2-enriched atmosphere?
6. How does rising atmospheric CO_2 concentration affect leaf temperature of C_3 plants?
7. Calculate light saturated photosynthesis for a C_3 plant with $V_{max} = 60$ μmol CO_2 m^{-2} s^{-1}, $J_{max} = 150$ μmol m^{-2} s^{-1}, $\Gamma_* = 3$ Pa, and $c_i = 25$ Pa. Assume $K_c = 30$ Pa, $K_o = 30\,000$ Pa, and $O_i = 20\,900$ Pa.
8. Using the same values as question 7, calculate light-saturated photosynthesis at $\phi = 2000$ μmol photons m^{-2} s^{-1}

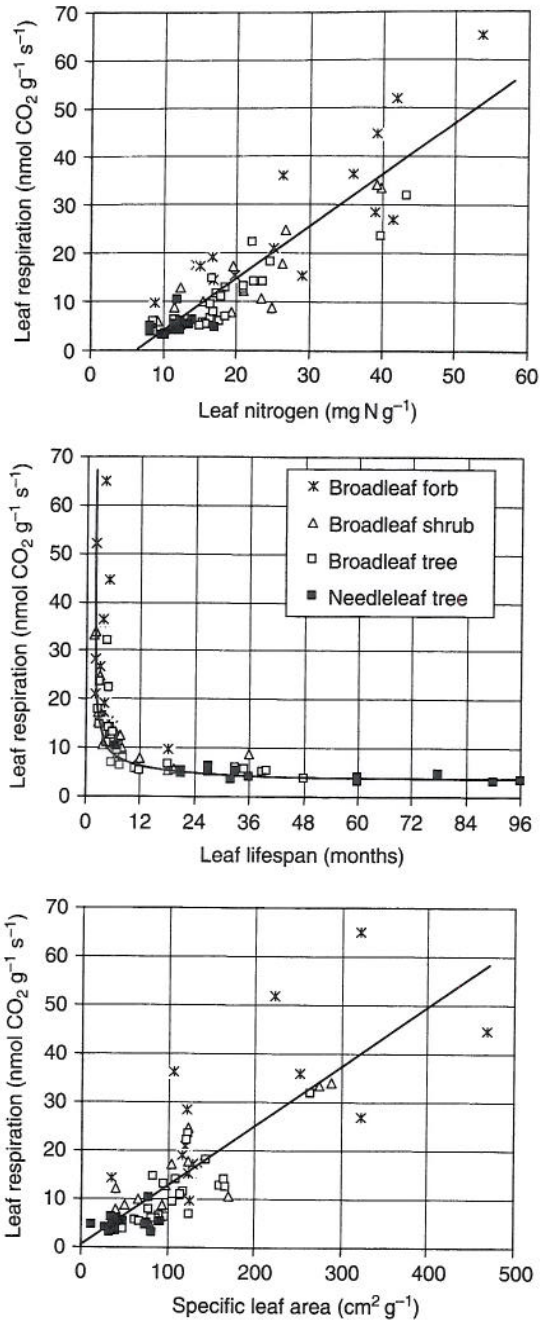

FIGURE 17.11. Relationships of leaf maintenance respiration at 25 °C to leaf nitrogen (top), leaf lifespan (middle), and specific leaf area (bottom) for 69 species of forbs, broadleaf shrubs, broadleaf trees, and needleleaf trees. Data from Reich *et al.* (1998b).

for the following values of V_{max} and J_{max}. For which value of V_{max} is it advantageous to have a high J_{max}? Is it advantageous to have high V_{max} in a sunny environment?

	J_{max} (μmol photons m^{-2} s^{-1})		
V_{max} (μmol CO_2 m^{-2} s^{-1})	75	150	300
30			
60			

9. Repeat question 8, but with low irradiance ($\phi = 100$ μmol photons m^{-2} s^{-1}). Is it advantageous to have high V_{max} in a shaded environment?
10. Based on coordinated leaf traits, which type of tree is expected to have larger maximum stomatal conductance: a broadleaf deciduous tree or a needleleaf evergreen tree? Why?

17.11 References

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